

## On the Taxonomic Affinities of the Dmanisi Mandible (Georgia)

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**ABSTRACT** The recent discovery of unexpectedly ancient human remains has fuelled interest about the first dispersion of *Homo* outside Africa. The Dmanisi mandible is perhaps one of the most interesting findings, as it supposedly represents one of the oldest hominids outside of Africa. Recently, different interpretations have been published about this specimen. Our comparison of the Dmanisi mandible with a large sample of mandibles and teeth has led us to a new interpretation. In our view, the Dmanisi mandible exhibits a unique combination of traits. Some of its features, taken in isolation, may be attributed to morphological extremes within the genus *Homo*. The architecture of the mandible as well as the morphology and dimensions of incisors, canines, and P3s are clearly primitive. However, dental traits such as the reduction of the talonid in the P4s and a distally decreasing molar series seems to be derived. Some combinations of these traits are found in specimens of *Homo ergaster* and differ from those generally present in later hominids. Thus, we propose that the Dmanisi mandible might be taxonomically classified as *Homo sp. indet. (aff. ergaster)*. Furthermore, some aspects of the dentition in Dmanisi display close similarities to Asian *Homo erectus*. If the 1.8–1.6 Myr dating for the Dmanisi mandible is correct, the differentiation of the Asian branch of the genus *Homo* could be regarded as a very ancient event. *Am J Phys Anthropol* 107:145–162, 1998.

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There is renewed interest in the first occurrence of *Homo* outside of Africa. The reason for this is twofold: the announcement of new dates for the oldest Asian human fossils at two Indonesian sites (Sangiran and Mojokerto), with isotopic ages as old as 1.6–1.8 Myr (Swisher et al., 1994), and the discovery of very ancient specimens in China (Longgupo Cave; Huang et al., 1995), in Europe (Atapuerca TD site; Carbonell et al., 1995a), and the Caucasus (Dmanisi, Georgia; Gabunia and Vekua, 1995a). Consequently, the human occupation of Eurasia is perceived by some as an event much older than previously envisioned. In the same way, there is ongoing debate about the earliest occupation of Europe (Roebroeks and van Kolfschoten, 1994; Carbonell et al., 1995b).

The clarification of the routes and patterns of the first dispersion of *Homo* outside Africa involve estimates of age and information on archaeological industries, faunal assemblages, and hominid characteristics. The issues are complex and identifying the taxonomic affinities of those first colonizers is a crucial matter.

The mandible from Dmanisi (East Georgia, Caucasus) warrants attention because the specimen was found in association with a Late Villafranchian (Late Pliocene to Early

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Pleistocene) faunal assemblage and a Mode 1 archaeological industry. Three independent methods date the mandible between 1.8–1.6 Myr ago (Gabunia and Vekua, 1995a; see also Dean and Delson, 1995). Current geophysics and faunal data place the Dmanisi mandible between 1.7–1.6 Myr and new paleomagnetic analysis is in preparation (Lordkipanidze, personal communication). Gabunia and Vekua (1995a,b) originally attributed the specimen to *H. erectus*. However, Bräuer and Shultz (1996) have recently concluded that the Dmanisi mandible shows closer morphological similarities with mandibular specimens younger than 1 Myr and classified it as later *H. erectus* (Bräuer, 1995). Thus, there seems to be a contradiction between the apparently derived morphology of the specimen and the remarkably ancient age attributed to it.

Certainly, the Dmanisi mandible displays an intriguing combination of traits. Some are undeniably primitive, while others appear very “advanced” (e.g., a decreasing molar series). These observations, coupled with an absence of an earlier conceptual framework on the occupations of the Caucasus, focus interest on the mandible. Our attention here is on some aspects of the specimen's morphology that have been previously overlooked. Simultaneously, we address some other features to elucidate the taxonomic affinities of the Dmanisi mandible.

## MATERIALS AND METHODS

The Dmanisi mandible was first exhibited in 1991 at the Senckenberg Institut colloquium in Frankfurt. Later, a detailed analysis was undertaken on casts in collections of the Natural History Museum (London) and the Laboratoire d'Anthropologie, University of Aix-en-Provence (France) (Fig. 1). The morphological terms used in this article are after Rosas (1995) for the mandible and after Bermúdez de Castro (1993) for the dentition.

### Comparison of the mandible

We compared the Dmanisi mandible with a large sample of teeth and mandibles of

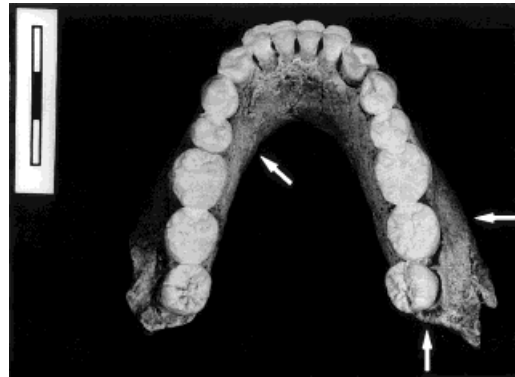


Fig. 1. The Dmanisi mandible (cast). The arrows indicate features of particular importance in this study.

*Australopithecus* and *Homo* (Table 1). The Atapuerca-SH sample is used as a baseline for the pattern of variability, as it is the largest Middle Pleistocene sample (Rosas, 1995, 1997). We follow Wood (1991, 1994) in the taxonomic attribution of East African mandibles of *Homo habilis* (OH 7, OH 13, OH 37, KNM-ER 1805), *Homo rudolfensis* (KNM-ER 1802), and *Homo ergaster* (KNM-ER 730, KNM-ER 731, KNM-ER 992, KNM-ER 1507). The mandible from the KNM-WT 15000 skeleton is included here in the latter taxon. We restrict the nomen of *H. erectus* to Asian hominid samples from China (Zhoukoudian, Lantian) and Indonesia (Sangiran). Nevertheless, these two Asian samples are largely considered independently in the comparisons. African samples from Olduvai (OH 22, OH 23, OH 51), Baringo (KNM-BK 67 and KNM-BK 8518), and South Africa (SK 45), as well as the North African specimens from Thomas I quarry and Tighenif are referred to by the local name of the samples, or treated as isolated specimens. In contrast to others (Rightmire, 1990; Bräuer, 1994), we think that the taxonomic status of these African samples needs resolution. Occasionally, we use the name *H. erectus s.l.* to include Asian and African samples other than *H. ergaster*. We designate European Middle Pleistocene and Neanderthal populations as “European clade” hominids, based on the hypothesis of an ancestor–descendent relationship (Stringer et al., 1984; Hublin, 1988; Trinkaus, 1988; Rosas et al., 1991). In this group, we further

TABLE 1. List of hominid fossils

Specimen/sample	Reference
Dmanisi	Gabunia and Vekua (1995a,b)
	Bräuer and Shultz (1996)
	White and Johanson (1982)
AL-288	
AL-266	
AL-400	
AL-333W-16	
AL-188-2	
AL-198-1	
AL-333w-1A	
AL-333-43	
LH-4	White (1977)
UR 501	Bromage et al. (1995)
OH 7, 13, 16, 24, 39	Tobias (1991)
KNM-ER 730	Day and Leakey (1973)
KNM-ER 992	Leakey and Wood (1973)
KNM-ER 730, 1802 (teeth)	Leakey et al. (1978)
KNM-ER 806, 820, 992 (teeth)	Leakey and Wood (1973)
KNM-ER 3734	Leakey et al. (1978)
KNM-WT 15000	Brown and Walker (1993), Walker and Leakey (1993)
SK 45	Broom and Robinson (1950)
OH 22, 23, 51	Rightmire (1980)
KNM-BK 67	Leakey et al. (1969)
KNM-BK 8518	Wood and van Noten (1986)
Sangiran 9	von Koenigswald (1968), Jacob (1973)
Sangiran 22	Sartono (1974)
Sanigran 1, Zhoukoudian	Weidenreich (1936), Wolpoff (1971)
Lantian	Woo (1964)
Tighenif (Ternifine)	Arambourg (1963)
Thomas I	Saussé (1975)
Rabat	Thoma and Vallois (1977)
Mauer	Wolpoff (1971)
Arago II & XIII	de Lumley et al. (1982)
Montmaurin	Billy and Vallois (1977)
Atapuerca (teeth)	Bermudez de Castro (1986; 1993)
Atapuerca (mandibles)	Rosas (1995), Rosas (1997)
Krapina J, G, H, E & C	Jelinek (1969), Smith (1976)
Krapina dental sample	Wolpoff (1979)
Chateaufort 2	Tillier (1979)
Arcy 2 and A9	Leroi-Gourhan (1958)
Circeo 3 and 4	Borgognini (1983)
La Quina 9, Spy 1 and 2	de Lumley (1973)
Le Moustier, Subalyuk, Ehringsdorf (adult and adolescent)	
Tabun	McCown and Keith (1939)
Vindija	Wolpoff et al (1981)
La Ferrassie	Heim (1976)
Regourdou	Piveteau (1963)
Amud	Suzuki and Takai (1970)
Ochoz	Vlcek (1969)
Monsempron b	Vallois (1952)
Shanidar	Trinkaus (1978, 1983)
Aboriginals from Granaria (Canary Islands)	Bermúdez de Castro (1985)

TABLE 2. Mesiodistal (MD) and buccolingual (BL) dimensions\* of the Dmanisi mandible

	I2	C	P3	P4	M1	M2	M3
MD	6.5	8.6	8.9	8.2	13.0	12.3	11.6
BL	6.6	8.2	9.7	9.9	12.7	11.9	10.8

\*These measurements were obtained from a cast (see text).

### Comparison of the dentition

Dental dimensions are of interest in hominid phylogenetic studies (Blumenberg and Lloyd, 1983). However, we believe that tooth shape analysis is a more powerful tool in phylogenetic research. Our approach used interdental indices involving the crown area (CA) (Bermúdez de Castro, 1986, 1993), a variable which was calculated from the mesiodistal (MD) and buccolingual (BL) dimensions of the teeth ( $CA = MD \times BL$ ). The MD and BL dimensions of the Atapuerca-SH, Arago, Montmaurin (mandible), Lazaret, Tighenif, Hortus, Malarnaud, Macassar-gues, La Ferrassie 2, and La Quina 5 original specimens were taken by JMBC to the nearest 0.1 mm, following Lefèvre's (1973) technique. Measurements from other specimens and samples were taken from the literature (Table 1). MD and BL dental dimensions of Dmanisi teeth were obtained from a good cast (Table 2). Our results are very similar to those obtained by Gabunia and Vekua (1995) and Bräuer and Schultz (1996) on the original specimen. The slight differences in measurements do not significantly distort the results of our shape analysis of the Dmanisi and other hominid teeth.

For a multivariate shape analysis we used the "WF" distance measure, a measure first described by Bermúdez de Castro (1993). MD and BL dimensions of the teeth are used in the calculation of the WF distance. We calculated from the BL and MD dimensions, respectively, a new variable  $X_A/((X_A + X_B)/2)$ , where  $X_A$  and  $X_B$  were the values of the variable  $X_i$  ( $i = 1, \dots, n$ ) in samples A and B, respectively. The shape distance, WF, between A and B ( $\$$ ) was defined as the variance of  $[X_A/((X_A + X_B)/2)]_i$ .  $\$ = 0$  expresses an identity in shape between A and B. In order to include the greatest number of specimens in this analysis, we used MD and BL dimensions of the lower I2, C, P3, P4, M1, and M2. From the dissimilarity matrix

distinguish two species: *H. heidelbergensis* and *H. neanderthalensis*. Finally, *Homo sapiens* refers to Upper Paleolithic samples and to all living human populations.

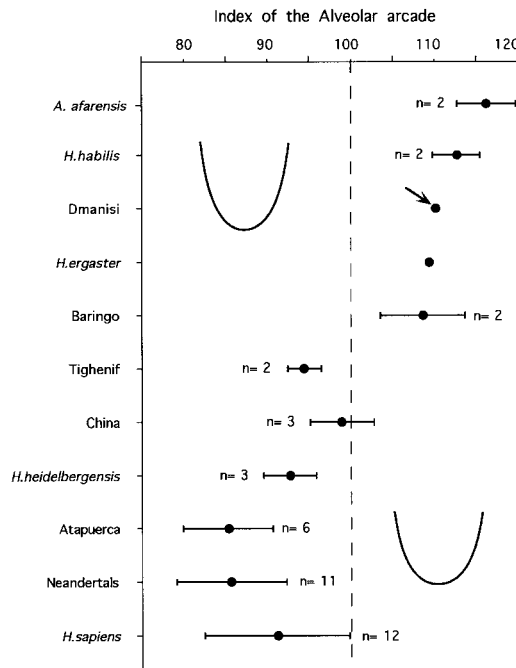


Fig. 2. Index of the alveolar arcade in a variety of hominid samples and specimens. The length of the arcade is measured as the distance from the infradentale point to the M3 (bucco-distal alveolar corner). The transversal dimension of the arcade is estimated as the bimolar M3 width.

obtained from the WF distance, the corresponding phenogram was generated (UPGMA method; Sneath and Sokal, 1973) using the NTSYS program (Rohlf, 1992). Following Rohlf (1992), the coefficient of "cophenetic correlation" was used as a measure of goodness of fit for the cluster analysis. The "cophenetic correlation" coefficient was obtained by comparing the cophenetic matrix (Rohlf and Sokal, 1981) and the original dissimilarity matrix upon which the clustering was based (product-moment correlation; Rohlf, 1992).

## RESULTS

### Shape of the alveolar arcade

The shape of the alveolar arcade related to the overall architecture of the skull. Figure 2 compares a length/width index of the alveolar arcade in a variety of mandibles (Table 3). The Dmanisi mandible presents an index similar to that of mandibles of *H. ergaster* and *H. habilis* average, and is

TABLE 3. Measurements of the alveolar arcade and identification of the individuals

Specimen	Width <sup>1</sup> M3-M3	Length <sup>2</sup> I-M3	Index
Dmanisi	60.5	66.7	110.2
<i>A. afarensis</i>			
AL288	60.4	67.7	112.0
AL400	61.7	74.1	120.0
Average	61.0	70.9	116.0
<i>H. habilis</i>			
OH13	59.0	68.2	115.5
KNM-ER1805	66.9	72.6	108.5
Average	62.9	70.4	112.0
<i>H. ergaster</i>			
KNM-ER992	64.3	70.4	109.4
Baringo			
KNM-BK8518	66.6	69.0	103.6
KNMBK67	58.2	66.2	113.7
Average	62.4	67.6	108.6
Tighenif			
TG 1	76.8	71.0	92.4
TG 3	75.2	72.6	96.5
Average	76.1	71.8	94.4
China			
ZHD G1	75.3	72.1	95.7
ZHD H1	59.7	61.8	105.5
Lantian	72.7	71.0	97.6
Average	69.2	68.3	99.6
<i>H. heidelbergensis</i>			
ARA II	71.3	64.0	89.7
Montmaurin	68.9	66.3	96.2
Mauer	70.9	65.5	92.3
Average	70.3	65.2	92.7
Atapuerca			
AT-1	72.5	61.3	84.5
AT-250	75.3	59.2	78.6
AT-505	65.4	58.5	89.4
AT-605	73.2	62.9	85.9
AT-888	70.1	62.7	89.4
AT-950	69.7	58.0	83.2
Average	71.0	60.4	85.1
<i>H. neanderthalensis</i>			
Krapina J	79.8	63.5	79.5
Krapina H	70.1	64.4	91.8
Ochoz	69.0	64.0	92.7
Amud 1	75.4	60.9	80.7
Tabun 1	69.8	59.7	85.5
Tabun 2	68.7	62.6	91.1
La Ferra.	66.6	60.0	90.0
Spy 1	73.9	59.9	81.0
Regourdou	71.4	59.3	83.0
Circeo 3	74.3	63.5	88.1
Kebara	77.0	62.4	81.0
Average	72.3	61.8	85.8
<i>H. sapiens</i>			
Average	68.0	62.5	91.9

<sup>1</sup> Width: bi-molar M3-M3 distance.

<sup>2</sup> Length: infradentale (ID)-M3 distance.

slightly lower than seen in OH 13. By contrast, younger samples from North Africa, China, Europe, and modern humans have index values below 100. Mandibles with an index about 100 generally display a narrow and broadly U-shaped arcade, as seen in specimens of *A. afarensis* (AL-400 and LH-4),



in early *Homo* specimens (OH 13 and OH 37), in the *H. ergaster* mandibles KNM-ER 992 and KNM-WT 15000, as well as in the Baringo sample (KNM-BK 67 and KNM-BK 8518). The Dmanisi mandible is included in this group. It is noteworthy that, with the exception of Dmanisi, all of these mandibles derive from East Africa. On the other hand, mandibles with an index lower than 100 display an alveolar arcade more parabolic in shape and, more importantly, a much wider M3 bimolar width. Within this latter group, however, the anterior part of the alveolar arcade displays variation. Thus, it is generally narrow in *H. erectus* mandibles, gently pointed in the Chinese specimens from Zhoukoudian and Lantian, and more gently curved in the Indonesian specimens. The alveolar arcade in the European clade mandibles is anteriorly fairly broad, with the P3 further aligned with the anterior dentition than with the cheek teeth. This is a condition which is maximized in Neanderthals.

Gabunia and Vekua (1995a,b) characterized the alveolar arcade of the Dmanisi mandible as narrow and broadly U-shaped, pointing out that the P3 is aligned with the cheek teeth. The shift between the anterior and lateral parts of the arcade is located at the level of the canine. These characteristics set the Dmanisi mandible clearly apart from the European clade mandibles, and show more similarities to those from *H. erectus*. However, the general shape of the alveolar arcade is certainly different. Thus, whereas some aspects of the alveolar arcade of the Dmanisi mandible seem to be general and thus shared with a variety of *Homo* specimens, the structure of the dental arcade clearly joins the Dmanisi mandible to the primitive form detected in *Homo* (Fig. 2). Henke et al. (1995) reached a similar conclusion. They detected strong affinities to *Australopithecus*, *H. habilis*, *H. rudolfensis*, and only marginal affinities to the *H. erectus* sample.

### Symphysis

A well-developed mental trigone (*trigonum mentalis*) is considered a derived feature in *Homo* (Leakey et al., 1964; Wood and van Noten, 1986; Bräuer and Schultz, 1996), although some early representatives of the

genus display a clearly discernible mental trigone (Day and Leakey, 1973; Tobias, 1991; Wood, 1991). The structure of the chin is classically divided into two main components: the *mentum osseum* and the mental trigone. Likewise, the mental trigone is further subdivided into mental protuberance and mental tubercles (Weidenreich, 1936; Tobias, 1991). A well-developed *mentum osseum* has been identified in the Dmanisi mandible by Gabunia and Vekua (1995b) and Bräuer and Shultz (1996) describe its chin area as a "clearly visible swelling of the symphyseal tuber." However, none of these authors conclude that a mental trigone is present in this specimen. We differ: in our view, the Dmanisi mandible exhibits a visible and prominent mental trigone. There is, however, no sign of mental fossae or lateral tubercles.

The existence of a mental trigone in the mandible of KNM-ER 730 has also received opposing interpretations. Whereas Day and Leakey (1973) identified a mental trigone, Rightmire (1990) did not recognize such a structure in KNM-ER 730. This difference of interpretation seems to be related to the presence or absence of lateral tubercles in a particular mandible. According to Rightmire (1990), a proper mental trigone is accompanied by lateral (mental) tubercles. In contrast, Tobias (1991) notes the presence of both *mentum osseum* and mental trigone in the *H. habilis* mandibles OH 13 and OH 7, none of which display lateral tubercles. Thus, it seems possible that a mental trigone without lateral tubercles developed early in the evolution of *Homo*, as OH 13, OH 7, KNM-ER 730, and the Dmanisi mandible illustrates.

With regard to the shape of the mental trigone and its relation to the anterior dentition, the Dmanisi mandible displays a shape similar to that of KNM-ER 730 and KNM-WT 15000, as has been noted by Gabunia and Vekua (1995a,b). There are, however, differences among *H. ergaster* mandibles. The chin region is gently rounded and receding in KNM-ER 992 (Rightmire, 1990) but a distinct mental trigone is recognized in KNM-ER 730 by Day and Leakey (1973); although Rightmire (1990) does not share this view. In immature specimens,

Walker and Leakey (1993) identify a very faint symphyseal tubercle in KNM-WT 15000, which is also recognizable in KNM-ER 820.

Mandibles of *H. erectus s.l.* often show a sloped symphysis, with a deep submental incisura. This led to the traditional view that the absence of a mental trigone in these hominids constituted the antecedent condition for *H. sapiens* and, therefore, the presence of a mental trigone is itself a derived feature. However, others regard the mental trigone as appearing early in the evolution of *Homo* (White et al., 1981; Tobias, 1991), and the trigone is particularly obvious in mandibles of *H. ergaster*. In fact, Wood (1992) includes among the derived traits of *H. ergaster*, shared with *H. sapiens*, "a more substantial basal component at the mandibular symphysis." A mental trigone also occurs in specimens from Zhoukoudian and Tighenif, although in *H. erectus* there is generally no incurvation of the bone between the alveolar border and the base (no *metum osseum*) (Rightmire, 1990). The Atapuerca-SH sample illustrates a pattern of variation in which the chin becomes more accentuated with the size of the mandible (Rosas, 1995, 1997). Therefore, the apparent derived morphology of the Dmanisi mandible is compatible either with *H. ergaster* or with progressive forms of archaic *H. sapiens* such as Témara, or even Neanderthals (e.g., Regourdou).

With respect to the posterior aspect of the Dmanisi symphysis, we disagree slightly with Bräuer and Shultz (1996). In our view, the Dmanisi mandible displays a morphology fairly similar to that of the *H. ergaster* mandibles KNM-ER 992 and KNM-WT 15000. In these mandibles, the superior transverse torus crosses the symphysis from one side to the other as a fairly prominent relief and extends laterally into a conspicuous alveolar prominence, and which gradually decreases in thickness and terminates at the level of M2. The superior transverse torus and its lateral extension gives rise, inward of the alveolar arcade, to the formation of a lingual arcade (Fig. 1). A direct observation of that pattern in the Dmanisi mandible is reminiscent of early *Homo* man-

dibles OH 13 and OH 37, as well as KNM-ER 992 and KNM-WT 15000. Mandibles of *H. erectus s.l.* show a superior transverse torus restricted to the symphysis and, in spite of its prominence, it lacks lateral extension.

### Medial aspect of the corpus

The relief of the medial aspect of the corpus seems to follow a consistent pattern of change during human evolution (Rosas, 1992). Thus, the posterior subalveolar fossa and the mylohyoid line are practically absent in mandibles of *Australopithecus* and early *Homo* (Rosas, 1985). In contrast, a deeply excavated subalveolar fossa with a sharp and prominent mylohyoid line appears in mandibles of *H. sapiens* and of *H. neanderthalensis*. Between these two extremes, a variety of forms are detected in *H. erectus s.l.*

The morphology of the medial aspect in the Dmanisi mandible approaches that of the primitive state. It shows a diffuse mylohyoid line, beginning about 9.8 mm below the M3 and descending slightly for a short stretch following the lower margin of the alveolar prominence. A similar pattern is found in KNM-ER 992, KNM-ER 730, and KNM-WT 15000, and it is also present in mandibles from Java and from Tighenif.

A more informative feature concerns the orientation of the medial wall of the corpus at the level of M2 and M3. This wall displays in the Dmanisi mandible an outward orientation, in such a way that the M3 tilts lingually, as noticed by Gabunia and Vekua (1995a) (Fig. 1). At that level, the subalveolar plane is flat and also inclined outward. An identical shape is found in KNM-ER 992, KNM-WT 15000, and Sangiran 9. By contrast, the subalveolar plane is wider and more vertically oriented in Sangiran 1 and in mandibles from Tighenif. A clearly different shape is seen in the Chinese mandibles. In these, the subalveolar fossa is very deep and a fairly reduced subalveolar plane takes the form of a true molar eminentia, especially conspicuous in ZHD H1 and in the Lantian specimen. Although the subalveolar plane is wider in the European clade man-

TABLE 4. Position of the anterior marginal tubercle and the lateral prominence in adult hominid fossil mandibles

	Anterior marginal tubercle	Lateral prominence
Dmanisi	C-P3	M1-M2
<i>A. afarensis</i>		
AL-288	Absent	M2
AL-266	Absent	M2
AL-400	Absent	M2
AL-333W-16	Absent	M2
AL-188-2	Absent	M2-M3
AL-198-1	Absent	M2-M3
AL-333w-1A	Absent	M2
AL-333-43	Absent	M1
LH-4	P3-P4	M2
<i>A. africanus</i>		
MLD2	Absent	M1-M2
MLD18	Absent	M2
MLD34	Absent	M2
MLD40	Absent	M2-M3
<i>H. habilis/H. rudolfensis</i>		
UR 501	C-P3?	M2
KNM-ER 1802	C-PE → P3-P4	M2
KNM-ER 1483	Absent	M2
KNM-ER 1501	?	M2
KNM-ER 1502	—	M2
OH 13	Absent	M2
OH 37	C-P3	M2
<i>H. ergaster</i>		
KNM-ER 992	Absent	M2
KNM-ER 730	P3	M2-M3
KNM-WT 15000	Absent	M1
KNM-ER 3734	Absent	M2-M3
<i>H. erectus</i>		
Sangiran 1	P4-M1	M2
Sangiran 9	C-P3 (P3)	M1
Sangiran 22	P3-P4	M2
ZHD G1	P4	M2-M3
ZHD H1	P3-P4	M2-M3
ZHD K1	P4?	M2-M3
LANTIAN	Absent	M2
Other African samples		
SK45	P4-M1	M2-M3
KNM-BK 67	Absent	M2-M3
KNM-BK 8518	Absent	M2
OH 22	Absent	M2
OH 51	P4	—
Tighenif 1	P3 (P3-P4)	M2
Tighenif 2	P4	M2-M3
Tighenif 3	P4	M3
Thomas 1	Absent	M2-M3
<i>H. heidelbergensis</i>		
Mauer	P4-M1	M3
Arago II	M1	M3
Arago XIII	P4-M1	M2-M3
Montmaurin	P4	M2-M3
AT-1	M1	M3
AT-75	—	M3
AT-172	P4-M1	M3
AT-250	M1	M3
AT-300	M1	M3
AT-505	P3-P4	M3
AT-605	P4-M1	M3
AT-607	P4-M1	M2-M3
AT-888	M1	M3
AT-950	M1	M3
<i>H. neanderthalensis</i>		
Eringsdorf F	M1	M3
La Chaise BD1	?	M3

TABLE 4. (continued)

	Anterior marginal tubercle	Lateral prominence
Krapina J	M1	M3
Krapina G	P4-M1	M2-M3
Krapina H	M1	M3
Krapina E	P4	M2-M3
Vindija 231	P4	M3
Vindija 205	P4-M1	M2-M3
Vindija 226	M1	M3
Amud 1	M1	M3
Tabun II	P3	M3
Tabun I	Absent	M3
La Ferrassie	M1	M3
Spy I	M1	Distal M3
La Quina 9	P3-P4	M3
Regourdou	P3-P4	Distal M3
Circeo III	Absent	M3
S. Cesaire	P4-M1	M3
Shanidar 4	M1	M3

dibles, a conspicuous subalveolar fossa is always present. In these features, the Dmanisi mandible is more similar to mandibles from Java and from East Africa.

#### Anterior marginal tubercle

The development of anterior marginal tubercles has been emphasized by Bräuer and Shultz (1996) as a significant trait of the Dmanisi specimen. As these authors pointed out, these tubercles are associated with a newly developed morphology of the corpus in the genus *Homo* (Aguirre and de Lumley, 1978). Thus, whereas mandibles of *Australopithecus* lack anterior marginal tubercles, well-developed tubercles are found in Pleistocene samples from Africa (e.g., Tighenif 2, OH 51), Java (e.g., Sangiran 1 y 22), and Europe (e.g., Mauer and Atapuerca-SH). The presence of these tubercles in early *Homo* is unclear, although OH 37 and KNM-ER 1802 display a thickening at the basal border which may be considered an anterior marginal tubercle. The Dmanisi mandible certainly displays prominent anterior marginal tubercles, leading Bräuer and Shultz (1996) to infer closer affinities of this mandible with the later *Homo* sample. However, these authors overlook the extremely advanced position of the anterior marginal tubercles in Dmanisi, situated below the C-P3. Table 4 shows the position of this structure in a variety of mandibles. The anterior marginal tubercles are located at the level of the P3 or

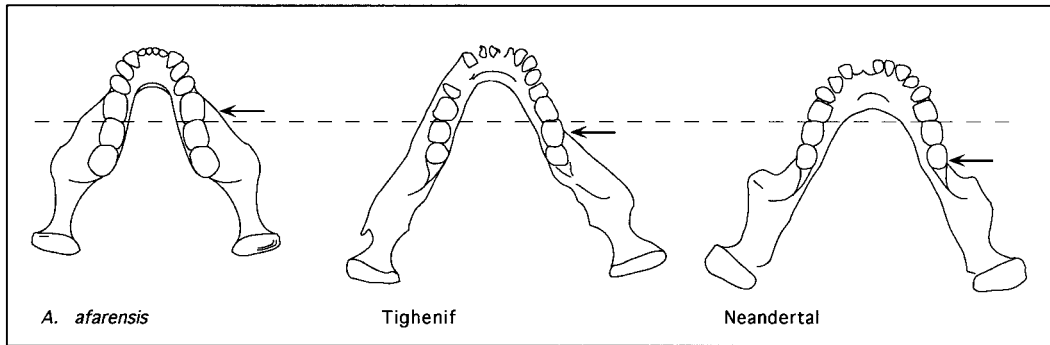


Fig. 3. The diagram compares the position of the lateral prominence (black arrows) and form of the corpus/ramus junction in mandibles of *A. afarensis* (left), Tighenif 3 (center), and a Neandertal (right). The dashed line indicates the position of the M1-M2 interseptum.

P3-P4 in all the Pleistocene mandibles, with the exception of the European hominids, in which these tubercles are located more posteriorly beneath the P4-M1. OH 37 displays the anterior marginal tubercle located below the C-P3, as it is located in the Dmanisi specimen, and KNM-ER 1802 exhibits a swelling of the basal border from the I2-C to P3-P4. On the other hand, the basal border is everted in Dmanisi, similar to the condition in KNM-ER 1802 and in OH 62, a trait Johanson et al. (1987) considered characteristic of *H. habilis*. We propose that the anterior marginal tubercles began their evolutionary differentiation below the canine in early *Homo* and subsequently migrated to more distal locations. The advanced position of the anterior marginal tubercles in the Dmanisi mandible would then be interpreted as a primitive trait, likening Dmanisi to early *Homo*. Whether or not this hypothesis is correct, the Dmanisi mandible displays anterior marginal tubercles in a location fairly different from that found in mandibles of *H. erectus s.l.*

#### Spatial relationship between the corpus and ramus

The form and location of the lateral prominence is of taxonomic value (Tobias, 1991; Rosas et al., 1991; Bräuer and Shultz, 1996). In our view, the lateral prominence of the Dmanisi mandible exhibits a primitive structure. In this specimen, the anterior border of the ramus expands anteriorly into a conspicuous lateral prominence, the maximum

thickness of which is located rather anteriorly below M1-M2. Table 4 displays the location of the lateral prominence in a variety of hominid mandibles. Although substantial variation is detected within the samples, a pattern can be defined. In the older mandibles, the lateral prominence is generally located in an anterior position below M2. The plane of the ramus is neatly positioned in a buccal position in relation to the corpus and the anterior border of the ramus passes rather anteriorly into the corpus. As a result, a voluminous lateral prominence and a wide extramolar sulcus are developed (Fig. 3). In lateral view, the ramus of these mandibles obscures M3 completely, or even part of M2. This pattern defines the primitive state for the hominid mandible and it is shared by *Australopithecus* and *H. habilis/H. rudolfensis* mandibles. As an extremely derived state, the mandibles from the European clade show the rami wholly aligned with the corpora and displaced backwards (Fig. 3). This new configuration of the corpus/ramus junction leads to, on the one hand, a weak lateral prominence disjunctive of the anterior ramal border and, on the other, a large retromolar space. Between the two extreme states described, samples of *H. erectus s.l.* display a large variation. Thus, in KNM-ER 992 and KNM-WT 15000, as well as in Sangiran 9 and Tighenif 1, the ramus is fairly separated from the corpus, leading to a prominent relief. In contrast, the lateral prominence takes the form of a rounded individualized swelling, distinct



from the anterior border of the ramus in KNM-ER 730, Sangiran 1, the Chinese mandibles, and in Tighenif 2 and 3. The most similar shape of the corpus/ramus junction of Dmanisi is found in KNM-WT 15000, in Tighenif 1, and in Sangiran 9; in the latter it is much more robust. The Dmanisi mandible maintains a primitive structure, fairly distinct from that of European hominids and other, later *H. erectus*.

The form of the retromolar area is closely related to the pattern of the corpus/ramus junction (Rosas, 1992). In the Dmanisi mandible, the triangular torus arises from just behind the M3, and it is oriented in a buccal direction, outward from the molar series (Fig. 1). Likewise, the internal wall of the corpus below M3 is clearly buccally oriented. As a result, nothing of a true retromolar area is developed in this mandible. Such an extreme morphology is only found in OH 13, where the root of the triangular torus is almost vertical (see Tobias, 1991). A similar pattern is observed in the mandibles of *A. afarensis* AL-400 and AL-228 as well as in those of *A. africanus* (MLD 18 and 40), perhaps with a slightly larger continuity of the alveolar margin behind the M3 in the latter. In a similar way, the specimen OH 37 presents the alveolar margin buccally oriented just behind the M3. It is not possible to assess this feature in mandibles of *H. ergaster* because of the preservation and juvenile condition of some specimens (KNM-ER 820 and KNM-WT 15000). By contrast, the alveolar margin behind the M3 of the *H. erectus s.l.* mandibles extends distally for a variable distance, to gently curve outward and upward. For instance, there are about 8 mm between the distal border of the M3 and the beginning of the triangular torus in Sangiran 21 and, in a lesser extension, in Sangiran 1B. Similarly, the mandible H1 from Zhoukoudian displays a large extension behind the M3, although this extension is much smaller in G1 and the Lantian mandible. The mandibles from Baringo show slightly different forms. A more homogeneous pattern is found in the African sample from Tighenif, and the specimens OH-22 and KNM-BK 67. In all of them, the alveolar margin behind the M3 extends backwards for a large extension, reaching a maximum

in Tighenif 3. This pattern is exaggerated in European clade hominids, where a large retromolar space is developed. In this way, a buccally oriented alveolar margin behind the M3, together with the triangular torus raising vertically from just behind the last molar defines the primitive condition in the hominid mandible. Thereby, the Dmanisi mandible shows a clearly primitive shape in regard to the corpus/ramus junction pattern.

### Tooth shape analysis

Table 5 shows the interdental indices obtained in the Dmanisi individual and other hominid specimens and samples. In Dmanisi, the CA C/P3 index is very low (81.7) and is similar to those obtained in KNM-ER 992, ZHD B1, and ZHD K1; the Dmanisi value is clearly greater than that obtained in OH 13 (69.7). The relatively small dimensions of the Dmanisi canine accounts for the low value for the CA C/P3 index in this specimen.

The Dmanisi mandible shows the CA P3 > P4 relationship, and shares this condition with KNM-ER 992, KNM-WT 15000, OH 22, and with the European clade hominids. In Zhoukoudian, the mean value of the CA P3/P4 index is less than 1, although some specimens (G1 and K1) show the P3 > P4 size sequence.

The data presented in Table 5 suggest that the size reduction of lower P4 was relatively greater than that of M1 from early *Homo* to recent modern humans. Unexpectedly, the Dmanisi tooth has a value for this index similar to that of modern humans, due to the relatively large size of the lower M1 in the Georgian specimen. Note that Tighenif 1, Thomas 1, and the Atapuerca SH sample have low values for this index as well.

The progressive increase of the CA M1/M2 index in genus *Homo* reflects the relatively greater size reduction of M2. The present evidence suggests that the CA M1 > M2 size relationship was reached in some hominid lineages during the Middle Pleistocene (OH 22, Atapuerca-SH, Zhoukoudian). The value of 112.8 obtained in the Dmanisi specimen is quite high; it is also due to the relatively great size of the M1. On the other hand, the size reduction of the M3 seems to be an early

TABLE 5. Interdental indices in the lower dentition of *Dmanisi* and other hominid specimens and samples

	CA C/CA P3 × (n, σ) Range	CA P3/AC P4 × (n, σ) Range	CA P4/CAM1 × (n, σ) Range	CAM1/CAM2 × (n, σ) Range	CAM2/CAM3 × (n, σ) Range	BL I2/BL M1 × (n, σ)
UR 501	—	114.9	60.9	71.3	—	—
OH7	88.0	85.1	64.7	85.7	—	—
OH 13	69.7	94.8	61.7	89.7	93.6	—
OH 16	—	99.9	65.5	76.3	107.6	59.1
OH 22	—	110.6	55.4	104.1	—	—
ER 730	—	—	—	—	93.1	—
ER 806	—	—	—	—	105.3	—
ER 820	—	—	—	—	—	62.0
ER 992	83.9	107.9	74.9	81.8	104.9	63.3
ER 1802	—	89.9	71.1	81.6	—	—
WT 15000	88.4	106.3	64.5	92.6	—	73.8
Dmanisi	81.7	106.3	49.2	112.8	116.8	51.9
Tighenif 1	—	101.2	51.5	91.1	115.2	—
Tighenif 2	—	92.8	57.6	91.9	113.6	—
Tighenif 3	89.5	107.3	56.2	98.4	116.4	59.8
Thomas I	—	—	51.3	91.9	135.2	—
Rabat	89.6	99.4	64.8	—	—	68.2
Sangiran B	—	—	62.3	94.7	94.0	—
Sangiran 9	—	102.7	—	—	103.1	—
Zhoukoudian	88.7 (4, 6.9) 82.8–95.4	97.6 (7, 6.9) 87.4–105.4	57.3 (5, 1.7) 55.3–59.9	102.8 (7, 7.0) 92.9–115.6	111.9 (6, 14.6) 99.2–135.7	63.2 (4, 4.7) 58.4–68.8
Montmaurin	—	—	—	102.4	91.8	—
Atapuerca-SH	94.9 (5, 7.7) 87.9–104.7	120.3 (9, 8.7) 106.1–136.2	51.0 (8, 5.1) 46.3–59.5	103.6 (11, 4.0) 97.1–108.7	104.0 (9, 7.5) 95.6–114.1	69.1* (3, —) 68.8–69.5
Arago 2	—	—	—	92.4	—	—
Arago 13	—	101.5	57.4	88.4	122.0	—
Mauer	93.8	105.6	53.1	85.2	114.7	69.6
Neandertals	99.5 (21, 6.9) 85.8–111.6	104.3 (22, 9.0) 89.0–121.7	53.9 (23, 5.0) 47.6–64.1	96.5 (25, 7.1) 85.5–113.4	106.7 (17, 14.9) 90.5–140.7	69.6 (16, 3.8) 63.8–78.1
Gran Canaria*	94.6 (126/264)	91.2 (264/297)	48.5 (297/504)	107.9 (504/507)	101.3 (507/440)	58.9 (73/504)

\* Values obtained from the ratio of the means of the samples.

BL: buccolingual; CA: crown area.

evolutionary trend in genus *Homo*. Thus, the CA M2 > M3 relationship occurs in OH 16, KNM-ER 806, KNM-ER 730, and KNM-ER 992 (Table 5). Therefore, the CA M2 > M3 relationship observed in Dmanisi may fit well with its supposed substantial antiquity. On the other hand, the high value of the CA M2/M3 index obtained in Dmanisi (116.8) indicates again the remarkable progressive condition of this specimen for the size reduction of the molar series.

The small BL dimensions of the Dmanisi incisors are comparable to those of KNM-ER 992 and Zhoukoudian. However, the great BL dimension of M1 in the Georgian specimen is comparable to values observed in OH 16, UR 501, KNM-ER 1802, as well as extreme Middle Pleistocene cases such as Arago XIII and Tighenif 1 and 2. This imbalance produces in the Dmanisi mandible a very low value for the BL I2/M1 index, clearly lower than that obtained in OH 16 (Table 5).

The phenogram determined after multivariate shape analysis in Figure 4 illustrates the relationships between the different hominid specimens and samples obtained from the corresponding matrix of dissimilarity (Table 6). Two main groups are distinguished in this phenogram: a group formed by the European hominids (Atapuerca-SH, Mauer, and the Neanderthals), Tighenif 3, and KNM-WT 15000, and another one formed by Zhoukoudian, KNM-ER 992, and the Dmanisi specimen. The values of the WF distance (Table 6) indicate that Zhoukoudian is the sample nearest to Dmanisi, whereas KNM-WT 15000 is the specimen more distant to Dmanisi. The European hominids are also very distant from Dmanisi.

In order to know what differences determine the WF distance values between Dmanisi and the other hominid specimens and samples, we analyzed the values of the expression  $X_A / ((X_A + X_B)1/2)$  for each one of

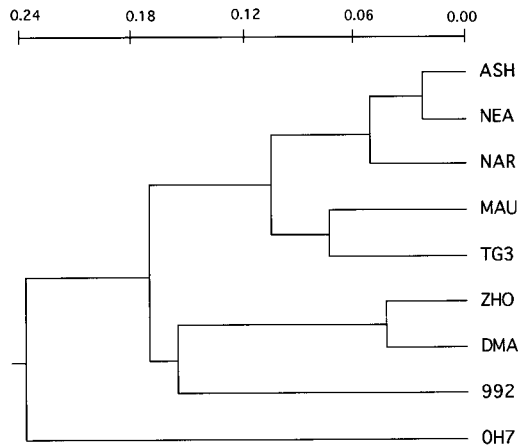


Fig. 4. Cluster formed from the WF dissimilarity matrix, using 12 variables (MD and BL of the I2-M2). Correlation between the cophenetic and original matrices:  $r = 0.81$ . Abbreviations of the samples as in Table 6.

the variables used in this study. The most important deviations of these, with respect to their respective means, contribute to a great extent to the variance and, therefore, to the WF distance. The Atapuerca-SH and Neanderthal samples, as well as the Tighenif 3 and KNM-WT 15000 specimens exhibit a common behavior when compared with Dmanisi. The most important deviations are obtained for the BL of the I2, C, and M1 (Table 7). Furthermore, the MD of the canine in Tighenif 3 and Mauer is proportionally much smaller than the same dimension in Dmanisi, whereas the MD of the I2 in this latter specimen is proportionally much smaller than the same variable in Atapuerca-SH and KNM-WT 15000.

The values set out in Table 7 (and Table 8) also offer a measure of the crown shape difference between each of the Dmanisi teeth and their homologs in other specimens and samples. The I2 and C of the Atapuerca-SH and Neanderthal samples, Mauer, and Tighenif 3 show very different values with respect to their MD and BL dimensions, indicating that in these hominids the crown shape of the I2 and C differs considerably from that of Dmanisi. These results also suggest that the increase of the BL dimensions of the anterior teeth, which characterizes European clade hominids, did not similarly affect the Dmanisi specimen.

The comparison between Dmanisi and OH 7 offers remarkable differences for seven of the twelve variables analyzed. The MD of P4 and M2, and the BL of C are proportionally much greater in OH 7, whereas the MD of the C and the BL of the P3, P4, and M1 are proportionally much greater in Dmanisi. Values obtained for the comparisons of the MD and BL of C, P3, P4, M1, and M2 differ considerably relative to each other and, therefore, the crown shape of these teeth is very different in OH 7 and Dmanisi.

The most important difference between Dmanisi and the Zhoukoudian sample concerns the C, P4, and M1 dimensions. The BL of C and the MD of P4 are proportionally smaller in Dmanisi, whereas the BL of the M1 is proportionally smaller in Zhoukoudian. The values obtained for the comparisons of the MD and BL of the C and M1 suggest a very different crown shape for these teeth in Dmanisi and the Zhoukoudian sample. Finally, the BL of the P3 is proportionally much greater in KNM-ER 992 than in Dmanisi, whereas the MD and BL of the M1 are proportionally much smaller in the African specimen. The crown shape of the P3 is very different in Dmanisi and KNM-ER 992, according to the values obtained for the comparison of the MD and BL of this tooth in both specimens. It is interesting to note that Dmanisi shares with OH 7, Zhoukoudian, and KNM-ER 992 a relatively small breadth of the lower incisors. Similarly, the BL dimension of the Dmanisi canine is also relatively small and, in this trait, the Georgian specimen only approaches OH 13 and KNM-ER 992.

In the previous analysis we observe that, except for OH 7, the M1 of Dmanisi is proportionally much greater than in the other hominid specimens and samples, thus confirming the results offered in Table 5 for the interdental indices. For this reason, we undertook a new shape analysis once the MD and BL of the M1 were removed from the database. In one-third of the cases we found similar WF values (differences less than 10%). In other cases, the WF values were somewhat different, but the increases or decreases were not greater than a 35%. However, the WF distance between Dmanisi and KNM-ER 992 decreased almost six times

TABLE 6. Values of the WF shape distance obtained from comparisons of Dmanisi (DMA) and other specimens

$\Phi$	DMA	ASH	MAU	NEA	TG3	NAR	992	ZHO
ASH <sup>1</sup>	0.186							
MAU <sup>2</sup>	0.188	0.078						
NEA <sup>3</sup>	0.209	0.019	0.038					
TG3 <sup>4</sup>	0.158	0.102	0.070	0.095				
NAR <sup>5</sup>	0.220	0.038	0.134	0.063	0.148			
992 <sup>6</sup>	0.184	0.206	0.232	0.241	0.166	0.143		
ZHO <sup>7</sup>	0.050	0.126	0.132	0.128	0.082	0.122	0.107	
OH7 <sup>8</sup>	0.196	0.279	0.237	0.259	0.216	0.217	0.264	0.118

<sup>1</sup> Atapuerca-SH (ASH).<sup>2</sup> Mauer (MAU).<sup>3</sup> Neandertals (NEA).<sup>4</sup> Tighenif 3 (TG3).<sup>5</sup> KNM-WT 15000 (NAR).<sup>6</sup> KNM-ER 992 (992).<sup>7</sup> Zhoukoudian (ZHO).<sup>8</sup> OH7.TABLE 7. Values<sup>1</sup> obtained on comparing the Dmanisi dental dimensions with those of other hominid specimens and samples

	OH7	ER 992	WT 15000	ZHO <sup>2</sup>	TIG3 <sup>3</sup>	MAU <sup>4</sup>	ATASH <sup>5</sup>	NEA <sup>6</sup>
I2								
MD	0.915	0.963	<b>0.903</b>	0.977	0.992*	1.015*	<b>0.992*</b>	0.995*
BL	0.943	0.978	<b>0.892</b>	0.978	<b>0.949</b>	<b>0.923</b>	<b>0.949</b>	<b>0.910</b>
C								
MD	<b>0.988*</b>	0.961	0.982*	1.000*	<b>1.048*</b>	<b>1.062*</b>	1.055*	1.042*
BL	<b>0.896</b>	<b>0.937</b>	<b>0.921</b>	<b>0.948</b>	<b>0.886</b>	<b>0.953</b>	<b>0.976</b>	<b>0.948</b>
P3								
MD	0.942	0.983*	0.983	1.017	1.005	1.047	1.059	1.059
BL	<b>0.979</b>	<b>0.928</b>	0.960	0.995	0.975	1.037	1.043	1.037
P4								
MD	<b>0.849*</b>	0.976	0.953	0.959	1.000	1.044	1.065	1.031
BL	0.961	0.943	0.990	0.970	0.985	1.036	1.070	1.042
M1								
MD	0.935*	<b>1.044</b>	<b>1.011*</b>	1.001	1.023	1.057	1.074	1.048
BL	<b>1.012</b>	<b>1.085</b>	<b>1.067</b>	1.028	<b>1.029</b>	<b>1.063</b>	<b>1.095</b>	<b>1.072</b>
M2								
MD	0.882*	0.964	0.976	0.992	0.988	0.984	1.056	1.016
BL	0.937	0.975	1.004	0.992	0.987	0.996	1.077	1.034
X	0.937	0.978	0.970	0.989	0.989	1.018	1.043	1.019
$\sigma$	0.044	0.043	0.047	0.022	0.040	0.043	0.046	0.046

Using the expression  $X_A/((X_A + X_B)^{1/2})_1$ , where  $X_A$  is the value of one of the  $i = 1 \dots n$  variables in Dmanisi and  $X_B$  the value of the variable in any of the other specimens and samples.

\* Differences between the values for the MD and BL dimensions equal or greater than  $1 \sum_{i=1}^n \sigma/n$ .

<sup>1</sup>In bold, values whose distance to its corresponding mean is equal or greater than  $1\sigma_{i=1}^n \sigma/n$ .

<sup>2</sup>ZHO: Zhoukoudian.

<sup>3</sup>TIG 3: Tighenif 3.

<sup>4</sup>MAU: Mauer.

<sup>5</sup>ATASH: Atapuerca-SH.

<sup>6</sup>NEA: Neandertals.

the previous value (0.184  $\rightarrow$  0.032), whereas the WF distance between Dmanisi and KNM-WT 15000 decreased 63% (0.220  $\rightarrow$  0.163). Therefore, the MD and BL dimensions of M1 contribute largely to establishing important shape differences between Dmanisi and the specimens included in *H. ergaster*. Similarly, the WF distance between Zhoukoudian and KNM-ER 992 decreased by 127%.

The phenogram shown in Figure 5 illustrates the new geometry of the relationships

between the different hominid specimens and samples. This geometry reflects the short shape distance between Dmanisi and KNM-ER 992 when the M1 dimensions are removed from the analysis.

### Some morphological dental traits

The most conspicuous feature of the canine of the Dmanisi specimen is the presence of a very broad and rounded median lingual ridge, which arises from an undeveloped basal swelling, and separates mesiolingual

TABLE 8. Crown index of the lower teeth in some Homo specimens and samples (mean values)

Specimen/sample	I2	C	P3	P4	M1	M2
OH 7	96.1	114.8	101.0	96.4	83.8	92.6
OH 13	—	93.8	95.8	103.1	89.2	87.0
OH 16	—	—	105.5	100.0	85.8	92.6
OH 22	—	—	94.0	117.6	90.7	91.3
UR 501	—	—	120.6	111.6	84.2	81.4
KNM ER 806	—	—	117.4	—	91.9	91.6
KNM ER 820	89.3	—	—	—	88.5	—
KNM ER 992	98.6	100.0	121.7	129.1	89.9	94.7
KNM ER 1802	—	—	107.5	105.3	87.8	85.4
WT 15000	103.8	107.8	114.1	112.2	87.4	91.5
Dmanisi	101.5	95.3	108.9	120.7	97.7	96.7
Tighenif 1	—	—	120.0	121.4	95.4	100.0
Tighenif 2	—	—	128.7	123.9	92.8	97.1
Tighenif 3	110.6	132.0	115.9	124.4	96.8	96.8
Casablanca	—	—	117.9	—	92.1	83.9
Rabat	107.1	111.8	111.1	105.5	91.7	—
Thomas 1	—	—	—	116.7	91.4	87.3
Sangiran 9	—	125.7	124.2	124.7	—	—
Zhoukoudian	101.1	105.6	114.0	118.1	93.9	96.8
	(n = 7, SD = 3.1)	(n = 8, SD = 5.8)	(n = 13, SD = 9.8)	(n = 8, SD = 10.8)	(n = 14, SD = 2.3)	(n = 11, SD = 5.3)
Mauer	122.2	118.4	111.1	122.7	96.5	94.5
ATA-SH	110.5	111.6	113.0	121.0	93.6	92.8
	(n = 14, SD = 6.1)	(n = 12, SD = 10.6)	(n = 14, SD = 3.9)	(n = 17, SD = 10.1)	(n = 19, SD = 3.6)	(n = 18, SD = 2.8)
Montmaurin	—	—	—	—	89.1	98.2
Arago2	—	—	—	—	99.1	91.6
Arago 13	—	—	128.9	132.9	94.2	95.2
Neandertals	118.1	114.2	114.5	118.4	93.5	92.9
	(n = 22, SD = 10.9)	(n = 30, SD = 7.7)	(n = 36, SD = 8.3)	(n = 40, SD = 11.4)	(n = 47, SD = 5.5)	(n = 38, SD = 5.4)
Gran Canaria	110.2	115.0	114.5	117.8	96.1	95.6
	(n = 73, SD = 8.2)	(n = 126, SD = 7.1)	(n = 264, SD = 7.0)	(n = 297, SD = 7.1)	(n = 504, SD = 4.2)	(n = 507, SD = 3.9)



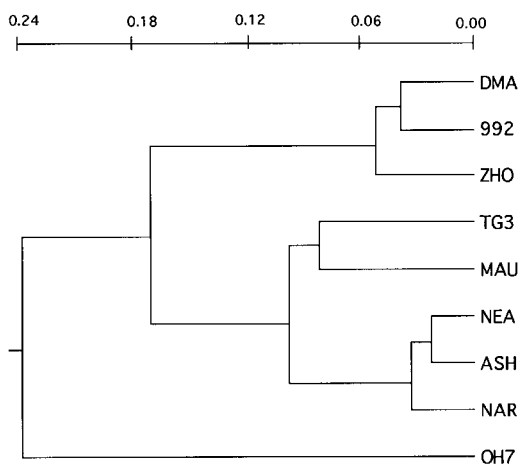


Fig. 5. Cluster formed from the WF dissimilarity matrix, using ten variables (MD and BL of the I2, C, P3, P4, and M2). Correlation between the cophenetic and original matrices:  $r = 0.87$ . Abbreviations of the samples as in Table 6.

gual and distolingual foveae. These foveae are limited by the mesial and distal marginal ridges, respectively. The morphology of this tooth closely resembles that of KNM-WT 15000 and KNM-ER 992.

In occlusal view, the crown of the Dmanisi P3 is clearly asymmetrical, especially due to development of the more lingual aspect of the distal marginal ridge. The lingual cusp is very low, and it is not well differentiated from the broad mesial and distal marginal ridges. This morphological pattern clearly differs from that observed in European hominids, such as Mauer, Arago, or Atapuerca-SH, whose P3s are more symmetrical and exhibit a small but well-differentiated lingual cusp. In contrast, the Dmanisi P3s have morphological similarities with those of African specimens, such as KNM-ER 992, OH 22, and Tighenif 1 and 2. The distal marginal ridge in the Dmanisi P4s forms a small talonid, which is clearly less developed than in other specimens, such as those of Zhoukoudian, Tighenif 2, and especially OH 7, OH 13, and OH 16. This accounts for the relatively shorter MD dimension of the P4s in the Georgian hominid. The single root of the Dmanisi P3s and P4s is a derived trait shared with early specimens (OH13, P4; KNM-WT 15000, P3 and P4; and KNM-ER

992, P4) and with the European clade hominids.

The large M1 of the Dmanisi mandible stands out against the other postcanine teeth. It is especially broad, due in part to the presence of a conspicuous protostylid on the buccal aspect of the protoconid. Enamel crenulations and secondary fissuration complicate to a great extent the morphology of the occlusal face of the molars, and which also exhibit accessory cusps: C7 on M1 and on M3, and C6 on M2 and on M3.

### DISCUSSION AND CONCLUSIONS

The Dmanisi mandible exhibits a unique combination of traits. In addition, the specimen displays some features that, taken one by one, may be attributed to morphological extremes within genus *Homo*. Thus, the architecture of the mandible is clearly primitive (see also Henke et al., 1995), while a set of dental traits seems to be derived. According to Gabunia and Vekua (1995a,b), the most reasonable interpretation of this specimen is that it belongs to a population of *H. erectus*. With regard to the structure of the Dmanisi mandible, we note in our analysis a close similarity with mandibles of *H. ergaster* or even with early *Homo* (*H. habilis*). The Dmanisi mandible is specially similar to KNM-WT 15000, in both the external and internal aspect of the symphysis and the corpus. The apparent derived morphology of the external symphysis, with a well-developed mental trigone, is fairly similar in both Dmanisi and the Nariokotome specimen. The immature condition of the Nariokotome boy does not seem to affect these features, as they are developed early in the postnatal growth period. The mandible KNM-ER 820, a younger individual than the Nariokotome boy (Smith, 1993), also shows a similar architecture.

The inclusion of KNM-WT 15000 in the taxon *H. ergaster* is currently under debate, as is this taxon in itself. The possible existence of a different species for the so-called African "erectus" was considered by Andrews (1984). Later, Clarke (1990, 1994) proposed the nomen *H. leakeyi* for the African "erectus" but Wood (1991, 1992) reintroduced the nomen *H. ergaster* (Groves and Mazak, 1975) as the most appropriated for

describing specifically the early African "erectus" (e.g., KNM-ER 992, KNM-ER 820, KNM-ER 730). In contrast, Rightmire (1986, 1990), Bräuer and Mbua (1992), and Bräuer (1994) do not consider it appropriate to split *H. erectus* into two separate species. According to them, the differences between African and Asian samples do not justify a distinct species. Walker and Leakey (1993) and Walker (1994) classify KNM-WT 15000 as *H. erectus*, even though they find close similarities of this specimen with KNM-ER 820, KNM-ER 992, and KNM-ER 730. The possibility that early African "erectus" might belong to a species other than *H. erectus* was considered by Walker and Leakey (1993). Were the possibility true, that species should be *H. ergaster*, following Wood (1991, 1994). Currently, a number of researchers (Tattersall, 1995; Larick and Ciochon, 1996) have accepted the species *H. ergaster*.

We also observe certain similarities with mandibles from Java and Tighenif 1, as did Gabunia and Vekua (1995a). These similarities concern primitive characters of the mandible. The largest similarities are found with robust specimens from Java. In contrast, the more gracile specimens Sangiran 1 and 22 do not show such close similarities; the same is true for the specimens from North Africa. Bräuer and Shultz (1996) state that the Dmanisi specimen exhibits clear affinities within the *H. erectus* range of variation, and they found closer similarities with the later *H. erectus* sample. In our view, the presence of anterior marginal tubercles in the Dmanisi mandible might best be evaluated with respect to their unusual location, and not attributed to morphological development alone. The location of these tubercles not only approaches that found in early representatives of *Homo*, but the anterior location of the lateral prominence and the shape of the retromolar area in Dmanisi also corresponds to the primitive pattern of the corpus/ramus junction. We therefore consider the structure of the Dmanisi mandible as very primitive and, hence, our interpretation differs from the taxonomic interpretation of Bräuer and Shultz (1996). In our view, Dmanisi does not display the typical shape of *Homo erectus* (s. str.).

On the other hand, the morphology and the relatively small breadth of the Dmanisi anterior teeth and of P3 suggest affinities of this specimen with early representatives of *Homo*, assigned either to *H. habilis* or to *H. ergaster*. The relatively small BL dimensions of the lower incisors in the Zhoukoudian sample also suggest certain affinities between Asian *H. erectus* and Dmanisi. This specimen would be progressive for the reduction of the talonid of the P4s, which produces an MD reduction of these teeth and contributes to the derived  $P3 > P4$  relationship. The derivation of this condition seems to occur very early in the evolution of African *Homo*, but, interestingly, the primitive condition,  $P4 > P3$ , characterizes the Zhoukoudian hominids. The M1 of Dmanisi is remarkably large, and this trait produces a derived pattern for the size relationships between this tooth and the others. This pattern is confused and certainly does not serve to clarify the phylogenetic relationships of the Dmanisi specimen. Thus, we found affinities either with the North African Middle Pleistocene (AC P4/M1), European late Middle and early Upper Pleistocene hominids (AC P4/M1; AC M1/M2), Zhoukoudian (AC M1/M2), or even with modern human (AC P4/M1; AC M1/M2; BL I2/M1). Our contradictory findings illustrate the difficulties encountered in dealing with isolated specimens. Nevertheless, multivariate dental shape analysis suggests a relationship of the Dmanisi hominid with certain Lower Pleistocene East African hominids and with Asian *H. erectus*.

Gabunia and Vekua (1995a) include in their conclusion that the Dmanisi mandible possibly foreshadows (European) early *H. sapiens*. In our analysis, no single trait is shared with the European clade hominids. A distally decreasing molar series is found in some samples from Europe (e.g., Atapuerca-SH), but this is a common trait developed in several Middle Pleistocene samples all over the world. Gabunia and Vekua (1995a) as well as Bräuer and Shultz (1996) consider the European Middle Pleistocene hominids as archaic *H. sapiens*. We, however, estimate these remains as representing populations belonging to a different species (*H. heidelbergensis*), defined by a set of apomorphic fea-

tures. None of these apomorphies are present in the Dmanisi mandible.

B. Wood has insisted that a combination of traits is the clearest expression of the distinctiveness of a species, and not the scale of expression for each of the characters taken in isolation (Wood, 1994). On the other hand, Wood (1992) considers *H. ergaster* as a taxon which retains several primitive characters (e.g., the form of the mandible) and shares derived features with *H. sapiens*. This definition fits perfectly with the Dmanisi mandible. The structure of the mandible is clearly primitive, while some traits of the dentition are especially similar to those of *H. sapiens*. In our view, the most reasonable classification for the Dmanisi mandible is *H. sp. indet. (aff. ergaster)*. The otherwise surprising similarity of the Dmanisi dentition with Asian *H. erectus* deserves special attention; new and more complete fossil remains could clarify the significance of these similarities. If an age of 1.8–1.6 Myr is broadly correct for the Dmanisi mandible, differentiation of the Asian branch of *Homo* may be regarded as a very ancient event indeed.

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#### LITERATURE CITED

- Aguirre E, and de Lumley MA (1978) Fossil man from Atapuerca, Spain: Their bearing on human evolution in the Middle Pleistocene. *J. Hum. Evol.* 6:681–738.
- Andrews P (1984) An alternative interpretation of the characters used to define *Homo erectus*. *Courier Forschungs-Institut Senckenberg, Frankfurt-Main*, 69: 167–175.
- Arambourg C (1963) Le gisement de Ternifine II. *L'Anthropologie mauritanicus*. *Arch. Inst. Paléont. Hum.*, Paris, Mém. 32:37–190.
- Bermúdez de Castro JM (1985) La Dentición de los Pobladores Prehistóricos de las Islas Canarias: Estudio Antropológico. Ph.D. Thesis. Universidad Complutense of Madrid.
- Bermúdez de Castro JM (1986) Dental remains from Atapuerca (Spain). *I. Metrics*. *J. Hum. Evol.* 15:265–287.
- Bermúdez de Castro JM (1993) The Atapuerca dental remains. New evidence (1987–1991 excavations) and interpretations. *J. Hum. Evol.* 24:339–371.
- Bermúdez de Castro JM (1995) Determinants of the dental variability in hominids. *Coloquios de Paleontología* 47:115–132.
- Billy G, and Vallois HV (1977) La mandibule pré-rissienne de Montmaurin. *L'Anthropologie* 81:273–312, 411–458.
- Blumenberg B, and Lloyd AT (1983) *Australopithecus* and the origin of the genus *Homo*: Aspects of biometry and systematics with accompanying catalog of tooth metric data. *BioSystems* 16:127–167.
- Borgognini SM (1983) A Neanderthal lower molar from Fondo Cattie (Maglie, Lecce). *J. Hum. Evol.* 12:383–401.
- Bräuer G (1994) How different are Asian and African *Homo erectus*? *Courier Forschungs-Institut Senckenberg, Frankfurt-Main*, 171:301–318.
- Bräuer G (1995) The Dmanisi mandible and its affinities to African and Asian Hominids. In: *Los Homínidos y su Entorno en el Pleistoceno Inferior y Medio europeo*. Congreso Internacional de Paleontología Humana. Orce, Granada, p. 96 (Abstract).
- Bräuer G, and Mbua E (1995) *Homo erectus* features used in cladistics and their variability in Asian and African hominids. *J. Hum. Evol.* 22:79–108.
- Bräuer G, and Schultz M (1996) The morphological affinities of the Plio-Pleistocene mandible from Dmanisi, Georgia. *J. Hum. Evol.* 30:445–481.
- Bromage TG, Schrenk F, and Zonneveld FW (1995) Paleoanthropology of the Malawi Rift: An early hominid mandible from the Chiwondo Beds, northern Malawi. *J. Hum. Evol.* 28:71–108.
- Broom R, and Robinson JT (1950) Man contemporaneous with the Swartkrans ape-man. *Am. J. Phys. Anthropol.* 8:151–156.
- Brown B, and Walker A (1993) The dentition. In A Walker and R Leakey (eds): *The Nariokotome Homo erectus Skeleton*. Berlin: Springer-Verlag, pp. 161–192.
- Carbonell E, Bermúdez de Castro JM, Arsuaga JL, Díez C, Rosas A, Cuenca-Bescós G, Sala R, Mosquera M, and Rodríguez XP (1995a) Lower Pleistocene hominids and artefacts from Atapuerca-TD6 (Spain). *Science* 269:826–829.
- Carbonell E, Mosquera M, Rodríguez XP, and Sala R (1995b) The First Human Settlement of Europe. *J. Anthropol. Res.* 51:107–114.
- Clarke RJ (1990) The Ndutu cranium and the origin of *Homo sapiens*. *J. Hum. Evol.* 19:699–736.
- Clarke RJ (1994) The significance of Swartkrans *Homo* to the *Homo erectus* problem. *Courier Forschungs-Institut Senckenberg, Frankfurt-Main*, 171:185–193.
- Day MH, and Leakey REF (1973) New evidence of the genus *Homo* from East Rudolf, Kenya. *I. Am. J. Phys. Anthropol.* 39:341–354.
- Dean D, and Delson E (1995) *Homo* at the gates of Europe. *Nature* 373:472–473.
- Gabunia L, and Vekua AK (1995a) A Plio-Pleistocene hominid from Dmanisi, East Georgia, Caucasus. *Nature* 373:509–512.
- Gabunia L, and Vekua AK (1995b) La mandibule de l'homme fossile du Villafranchien supérieur de Dmanisi (Géorgie Orientale). *L'Anthropologie* 99:29–41.

- Groves CP, and Mazak V (1975) An approach to the taxonomy of the Hominidae: gracile Villafranchian hominids of Africa. *Cas. Miner. Geol.* 20:225–247.
- Heim JL (1976) Les hommes fossiles de La Ferrassie. *Arch. Inst. Paléont. Hum.*, Paris, Mém. 35.
- Henke W, Roth H, and Simon C (1995) Qualitative and quantitative analysis of the Dmanisi mandible. In RJ Radlanski and H Renz Marketing (eds): *Proceedings of the 10th International Symposium on Dental Morphology*. Berlin: Marketing-Serveces, pp. 459–464.
- Howell FC (1960) European and Northwest African Middle Pleistocene hominids. *Curr. Anthropol.* 1:195–232.
- Huang W, Gu Y, Ciochon R, Larick R, Qiren F, de Vos J, Schwarcz H, Rink W, and Yonge C (1995) Early *Homo* and associated artifacts from Asia. *Nature* 378:275–278.
- Hublin JJ (1988) Les presapiens européens. *L'Homme de Neandertal*. Vol 3, L'Anatomie. Liège: ERAUL, no. 30, pp. 75–80.
- Jacob T (1973) Palaeoanthropological discoveries in Indonesia with special reference to the finds of the last two decades. *J. Hum. Evol.* 2:473–485.
- Jelinek J (1969) Neanderthal Man and *Homo sapiens* in Central and Eastern Europe. *Curr. Anthropol.* 10:475–503.
- Johanson DC, Masao TF, Eck GG, White TD, Walter RC, Kimbel WH, Asfaw B, Manega P, Ndessokia P, and Suwa G (1987) New partial skeleton of *Homo habilis* from Olduvai gorge, Tanzania. *Nature* 327:205–209.
- Koenigswald GHR (1968) Observations upon two *Pithecanthropus* mandibles from Sangiran, Central Java. *Proc. Koninkl. Nederl. Akad. Wetensch. Series B*, 71:99–107.
- Larick R, and Ciochon RL (1996) African emergence and early Asian dispersals of the genus *Homo*. *Sci. Am.* 84:538–551.
- Leakey REF, and Wood BA (1973) New evidence of the genus *Homo* from East Rudolf, Kenya. II. *Am. J. Phys. Anthropol.* 39:355–368.
- Leakey LBS, Tobias PV, and Napier, JR (1964) A new species of the genus *Homo* from Olduvai Gorge. *Nature* 202:7–9.
- Leakey LBS, Tobias PV, Martyn JE, and Leakey REF (1969) An Acheulean industry with prepared core technique and the discovery of a contemporary hominid mandible at Lake Baringo, Kenya. *Proc. Prehist. Soc.* 25:48–76.
- Leakey REF, Leakey MG, and Beherensmeyer AK (1978) The hominid catalogue. In MG Leakey and REF Leakey (eds): *Koobi Fora Research Project, Vol. 1: The Fossil Hominids and an Introduction to Their Context, 1968–1974*. Oxford: Clarendon Press, pp. 86–182.
- Lefèvre J (1973) Etude odontologique des hommes de Muge. *Bull. Mém. Soc. Anthropol.*, Paris, 12:301–333.
- Leroi-Gourhan A (1958) Etude des restes humaines fossiles provenant des grottes d'Arcy-sur-Cure. *Ann. Paleont.*, Paris, 44:87–148.
- Lumley MA de (1973) Anténeandertaliens et Néandertaliens du Bassin Méditerranéen occidental européen. *Etud. Quat. Mém.* 2.
- Lumley de H, Lumley de MA, and Fournier A (1982) La mandibule de l'homme de Tautavel. *Proc. 1er Congrès Int. de Paléon. Hum.* 2:178–221.
- McCown T, and Keith A (1939) The Stone Age of Mount Carmel. II. The Fossil Human Remains from the Levallois-Mousterian. Oxford: Clarendon Press.
- Piveteau J (1963) La grotte de Regourdou (Dordogne): paléontologie humaine. *Ann. Paleont.*, Paris, 49:285–304.
- Rightmire GP (1980) Middle Pleistocene hominids from Olduvai Gorge, Northern Tanzania. *Am. J. Phys. Anthropol.* 53:225–241.
- Rightmire GP (1986) Species recognition and *Homo erectus*. *J. Hum. Evol.* 15:823–826.
- Rightmire GP (1990) *The Evolution of Homo erectus*. Cambridge: Cambridge University Press.
- Roebroeks W, and van Kolfschoten T (1994) The earliest occupation of Europe. A short chronology. *Antiquity* 68:489–523.
- Rohlf FJ (1992) NTSYS-pc. Numerical Taxonomy and Multivariate Analysis System (Computer Program Manual). New York: Exeter Software.
- Rohlf FJ, and Sokal KK (1981) Comparing numerical taxonomic studies. *Syst. Zool.* 30:459–490.
- Rosas A (1985) Estudio morfológico y comparativo de los fragmentos mandibulares AT-83 y AT-75 del yacimiento de Atapuerca y análisis de polaridad de algunos rasgos mandibulares. MS Thesis, Complutense University, Madrid.
- Rosas A (1992) Ontogenia y Filogenia de la mandíbula en la evolución de los homínidos. Aplicación de un modelo de morfogénesis a las mandíbulas fósiles de Atapuerca. PhD Thesis. Complutense University, Madrid.
- Rosas A (1995) 17 New mandibular specimens from the Atapuerca/Ibeas Middle Pleistocene hominids sample (1985–1992). *J. Hum. Evol.* 28:533–559.
- Rosas A (1997) A gradient of size and shape for the Atapuerca sample and Middle Pleistocene hominid variability. *J. Hum. Evol.* 33:319–331.
- Rosas A, Bermúdez de Castro JM, and Aguirre E (1991) Mandibules et dents D'Ibeas (Espagne) dans le contexte de l'évolution humaine en Europe. *L'Anthropologie* 4:89–102.
- Sartono S (1974) A new discovery of hominid remains from Sangiran, Central Java. *Berita Direkt. Geol. Goesurv. News* 62:2–3.
- Saussé F (1975) Mandibule de la carrière Thoma I (Casablanca). *L'Anthropologie* 79:81–112.
- Smith FH (1976) The Neanderthal remains from Krapina: A descriptive and comparative analysis. Department of Anthropology, the University of Tennessee, Knoxville, TN. Reports of Investigation No. 15.
- Smith BH (1993) Physiological age of KNM-WT 15000. In A Walker and R Leakey (eds): *The Nariokotome Homo erectus Skeleton*. Berlin: Springer-Verlag, pp. 221–233.
- Sneath PHA, and Sokal RR (1973) *Numerical Taxonomy*. San Francisco: WH Freeman.
- Stringer CB (1984) Current issues in modern human origins. In WE Meikle, FC Howell, and NG Jablonski (eds): *Contemporary Issues in Human Evolution*. California Academy of Sciences, memoir 21, pp. 115–134.
- Stringer CB, Hublin JJ, and Vandermeersch B (1984) The origin of anatomically modern humans in western Europe. In: *The Origins of Modern Humans: A World Survey of the Fossil Evidence*. New York: Alan R. Liss, pp. 51–135.
- Suzuki H, and Takai F (1970) *The Amud Man and His Cave Site*. Tokyo: Academic Press of Japan.
- Swisher CC III, Curtis GH, Jacob T, Getty AG, Suprijo A, and Widiasmoro (1994) Age of the earliest known hominids in Java, Indonesia. *Science* 263:1118–1121.
- Tattersall I (1986) Species recognition in human paleontology. *J. Hum. Evol.* 15:165–176.
- Tattersall I (1995) *The Fossil Trail*. Oxford: Oxford University Press.
- Thoma A, and Vallois HV (1977) Les dents de l'Homme de Rabat. *Bull. Mém. Soc. Anthropol.* 13:31–58.
- Tillier AM (1979) La dentition de l'enfant moustérien Chateaufort 2 découvert à l'Abri de Hauteroche (Charente). *L'Anthropologie* 83:417–438.



- Tobias PV (1991) Olduvai Gorge. Vol. 4: The Skulls, Endocasts and Teeth of *Homo habilis*. Cambridge: Cambridge University Press.
- Trinkaus E (1978) Dental remains from the Shanidar adult Neanderthals. *J. Hum. Evol.* 7:369–382.
- Trinkaus E (1983) The Shanidar Neanderthals. New York: Academic Press.
- Trinkaus E (1988) The evolutionary origins of the Neanderthals or, Why were there Neanderthals? *L'Homme de Neandertal*. vol 3, L'Anatomie, Liège: ERAUL, no. 30, pp. 11–29.
- Vallois HV (1952) Les restes humaines du gisement Mousterian de Monsempron. *Ann. Paléont.*, Paris, 38:100–120.
- Vlcek E (1969) Neandertaler der Tschechoslowakei. Prague. Prague: Verlag der Tschechoslowakischen Akademie der Wissenschaften.
- Walker A (1993) Perspectives on the Nariokotome discovery. In A Walker and R Leakey (eds): *The Nariokotome Homo erectus* Skeleton. Berlin: Springer-Verlag, pp. 411–430.
- Walker A, and Leakey REF (1993) The skull. In A Walker and R Leakey (eds): *The Nariokotome Homo erectus* Skeleton. Berlin: Springer-Verlag, pp. 63–94.
- Weidenreich F (1936) The mandibles of *Sinanthropus pekinensis*: A comparative study. *Paleont. Sin.* (new series) 7:1–162.
- White TD (1977) New fossil hominids from Laetolil, Tanzania. *Am. J. Phys. Anthropol.* 46:197–230.
- White TD, and Johanson DC (1982) Pliocene hominid mandibles from the Hadar formation, Ethiopia: 1974–1977 collections. *Am. J. Phys. Anthropol.* 57:501–544.
- White TD, Johanson DC, and Kimbel, WH (1981) *Australopithecus africanus*: Its phyletic position reconsidered. *S. Afr. J. Sci.* 77:445–470.
- Wolpoff MH (1971) *Metric Trends in Hominid Dental Evolution*. Cleveland: Case Western Reserve University Studies in Anthropology 2.
- Wolpoff MH (1979) The Krapina dental remains. *Am. J. Phys. Anthropol.* 50:67–114.
- Wolpoff MH, Smith FH, Males M, Radovic J, and Rukavina D (1981) Upper Pleistocene human remains from Vindija Cave, Croatia, Yugoslavia. *Am. J. Phys. Anthropol.* 54:499–545.
- Woo J (1964) Mandible of *Sinanthropus lantianensis* in Shensi Province, China. *Curr. Anthropol.* 5:98–101.
- Wood BA (1991) Koobi Fora Research Project. Vol. 4. *Hominid Cranial Remains from Koobi Fora*. Oxford: Clarendon Press.
- Wood BA (1992) Early hominid species and speciation. *J. Hum. Evol.* 22:351–365.
- Wood BA (1994) Taxonomy and evolutionary relationships of *Homo erectus*. *Courier Forschungs-Institut Senckenberg, Frankfurt-Main*, 171:159–165.
- Wood BA, and van Noten FL (1986) Preliminary observations on the BK 8518 mandible from Baringo, Kenya. *Am. J. Phys. Anthropol.* 69:117–127.